NOAA Technical Report NMFS 132

January 1998

Stock Composition of Some Sockeye Salmon, *Oncorhynchus nerka*, Catches in Southeast Alaska, Based on Incidence of Allozyme Variants, Freshwater Ages, and a Brain-Tissue Parasite

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The *NOAA Technical Report NMFS* (ISSN 0892-8908) series is published by the Scientific Publications Office, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115-0070.

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Suggested reference
Pella, Jerome, Michele Masuda, Charles Guthrie III, Christine Kondzela, Anthony Gharrett, Adam Moles, and Gary Winans. 1998. Stock composition of some sockeye salmon, *Oncorhynchus nerka*, catches in southeast Alaska, based on incidence of allozyme variants, freshwater ages, and a brain-tissue parasite. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 132, 23 p.

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Stock Composition of Some Sockeye Salmon, *Oncorhynchus nerka*, Catches in Southeast Alaska, Based on Incidence of Allozyme Variants, Freshwater Ages, and a Brain-Tissue Parasite

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ABSTRACT

The incidence of four discrete characters of individual sockeye salmon —two genetically inherited proteins (*PGM-1** and *PGM-2**), freshwater age at migration, and the presence of the brain-tissue parasite *Myxobolus arcticus*—in weekly samples from two Alaskan fisheries (Noyes Island in 1986 and Sumner Strait in 1987) were used to infer stock composition of the catches based on corresponding character samples from 73 Alaskan and Canadian stocks. Estimated contributions of 13 stock groups, formed on the basis of character similarity of their members, were roughly consistent with expectations from tagging experiments, knowledge of stock magnitudes, and similar assessments from scales. Imprecision of the estimated contributions by the 13 stock groups limited their practical value; but variability was much reduced for combined estimated contributions by two inclusive categories, namely stock groups whose members had either high or low brain-parasite prevalence. Noyes Island catches consisted predominantly of unparasitized fish, most of which were probably of Canadian origin. The majority of Sumner Strait catches consisted of parasitized fish, whose freshwater origins may have been in Alaska or Canada.

Introduction

Salmon, *Oncorhynchus* spp., caught in fisheries of the northern boundary area (NBA) of southern Southeast Alaska and northern British Columbia (Fig. 1) comprise stocks of both U.S. and Canadian origin. In order to study the population dynamics of large individual stocks or stock groups and to assess the catches of either country's stocks taken by the other country's fisheries, the origins of salmon caught in NBA fisheries must be determined. This study examines the use of multiple (four) traits of individual sockeye salmon, *O. nerka*—two allozymes, freshwater age, and a brain-tissue parasite—with mixture model analysis (Fournier et al., 1984; Pella and Milner, 1987) in order to estimate the stock composition of catches for two Alaskan fisheries and compares these results with those from traditional methods, including tagging and scale-pattern analysis.

One of the guiding principles of the Pacific Salmon Treaty of 1985 between the United States and Canada was that each country should receive benefits from its fisheries equivalent to its own salmon production. Future agreements on salmon harvesting between the two countries will probably retain this concept. Because both U.S.- and Canadian-origin salmon are commonly caught together in coastal fisheries of each country, origins of salmon in coastal fisheries must be determined so that the salmon production by each country can be assessed. Determining the stock origins of salmon catches has been the focus of coastwide research supported under the treaty.

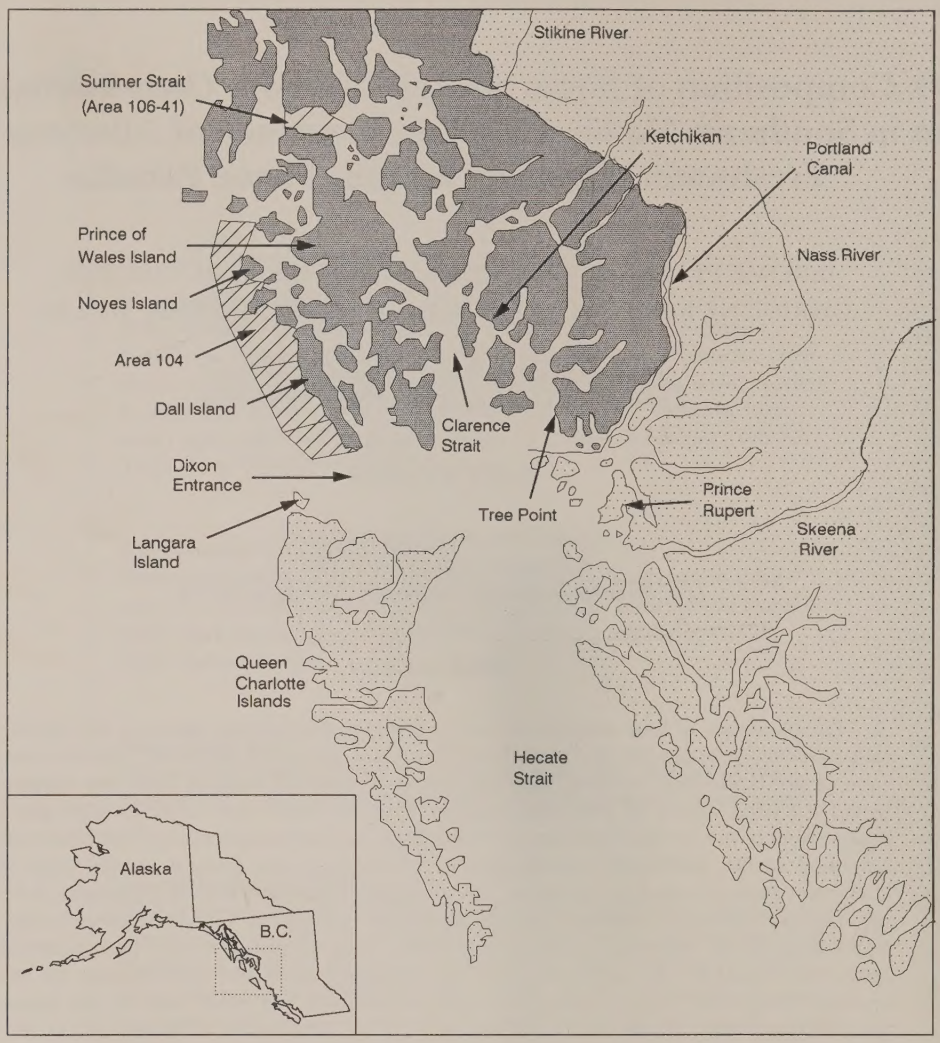

Figure 1
Boundary area of southern Southeast Alaska (dark) and northern British Columbia (dots). (Fisheries considered are indicated by striped areas.)

From 1982 to 1985, the Auke Bay Laboratory (ABL) of the U.S. National Marine Fisheries Service (NMFS) conducted joint research with the Alaska Department of Fish and Game (ADF&G) and the Pacific Biological Station (PBS) of the Canada Department of Fisheries and Oceans (CDFO) to determine stock composition of salmon catches in fisheries of the NBA. The goal was to evaluate the numbers of fish produced in Canada that are intercepted by U.S. fishermen and the numbers of fish produced in the U.S. that are intercepted by Canadian fishermen and also to develop further information for improved management of stocks that contribute to NBA fisheries. Initially, large-scale tagging experiments on adult sockeye salmon and pink salmon, *O. gorbuscha*, in NBA fisheries provided estimates of stock contributions (Pella et al., 1993; Gazey et al.[1]; English et al.[2]). However, stock composition in NBA fisheries varies among years owing to natural fluctua-

[1] Gazey, W. J., J. Taylor, K. K. English, T. Webb, and D. A. Birdsall. 1883. Part B: 1982 North coast tagging study. *In* W. J. Gazey and D. A. Birdsall (eds.), Design and execution of a stock interception study. Unpubl. rep. by LGL Limited and ESSA Environmental Social Systems Analysts Ltd., for Fisheries and Oceans, Canada, 107 p. [Available from LGL Limited, No. 333, 2453 Beacon Ave., Sidney, B.C., Canada.]

[2] English, K. K., W. J. Gazey, and J. A. Taylor. 1984. Part C: The 1983 North coast tagging study. *In* W. J. Gazey and D. A. Birdsall (eds.), Design and execution of a stock interception study. Unpubl. rep. by LGL Limited and ESSA Environmental Social Systems Analysts Ltd., for Fisheries and Oceans, Canada, 115 p. [Available from LGL Limited, No. 333, 2453 Beacon Ave., Sidney, B.C., Canada.]

tions in the relative magnitudes of contributing stocks. Furthermore, changes in oceanographic conditions probably affect migration routes of returning adult salmon (Blackbourn, 1987). If so, the phenomenon of el Niño, which occurs with varying intensity at 2–7 yr intervals and affects ocean temperatures over much of the Pacific coast, could cause irregular and varying disturbances of annual stock composition in NBA fisheries (Hamilton and Mysak, 1986). Therefore, estimates of stock contributions to NBA fisheries, if based primarily on information from the few years of adult tagging, are less reliable for nontagging years than for tagging years. Tagging experiments are prohibitively expensive for routine evaluation of stock composition in NBA fisheries if the annually changing stock mixtures are to be monitored; therefore, other methods are required. To this end, research has been directed toward determining stock composition of catches from attributes of sampled individuals.

Knowledge of attributes useful for determining stock composition of mixed sockeye salmon stocks in NBA fisheries has grown considerably since the initial tagging experiments. Researchers of ADF&G discovered that certain growth features on scales of sockeye salmon from coastal systems of Southeast Alaska differed from those on scales of sockeye salmon from large river systems—Nass, Skeena, and Stikine Rivers—where spawning grounds are in the interior of northern British Columbia (Marshall et al., 1984). As a result of this finding, use of scales to assess composition of sockeye salmon catches in Southeast Alaskan NBA fisheries has been routine since 1982.

These mixed-stock analyses based on scales have identified contributions of, at most, five major groups of stocks: 1) Southeast Alaska; 2) Nass River; 3) Skeena River; 4) Stikine River; and 5) south coast stocks, including those of the large Canadian Fraser River. Estimation of contributions by important component stocks within Southeast Alaska or from the Stikine River was attempted in some years. Which particular groups, or important component stocks, are included in an analysis depend on the fishery and year in which mixed-stock samples are assessed and are chosen with the intent of separating the main contributors. However, substantial Canadian stocks of the central coast of British Columbia, as well as numerous lesser populations of both Southeast Alaska and British Columbia that may occur in NBA fisheries, are not included.

Furthermore, growth patterns on scales used to identify stock origin vary annually because growth of salmon, recorded in the scale patterns, is affected by environmental conditions. Such variations in growth patterns can bias estimates of stock composition if the samples used for developing classification rules come from years different from those when the catch samples were taken. Consequently, scales of contributing stocks must be monitored annually (Jensen and Frank, 1988; Wood et al., 1989) as is currently done by ADF&G. To reduce costs due to annual sampling and thereby permit broader coverage of potentially contributing stocks, more time-stable characters, which do not require frequent resampling of contributing stocks, continue to be sought even though scales remain at present the practical basis of assessment.

Genetic characters are quite stable over periods of repeated sampling of salmon populations and can in principle be used for the assessment of mixed-stock composition (Milner et al., 1985). The basis for estimating stock composition is the variation in relative frequencies of inherited protein types. Such genetic differences among stocks of salmon are determined by electrophoretic assay of enzymatic proteins and have been useful in assessment of mixed stocks (Grant et al., 1980; Okazaki, 1981; Miller et al., 1983; Beacham et al., 1985; Utter et al., 1987; Shaklee et al., 1990a; Wishard[3]). Utter and Hodgins (1970) first described phosphoglucomutase polymorphism in sockeye salmon; and an initial survey of sockeye salmon stocks occurring in NBA fisheries (Utter et al.[4]) revealed that the two coding loci—phosphoglucomutase-1 and -2 (*PGM-1** and *PGM-2** in the nomenclature of Shaklee et al., 1990b)—had variation within and among populations.

Just as protein genetic characters can be effective for assessing mixed-stock composition, other biological characters observable in individuals can be useful, especially if the characters are fairly stable over time. Parasites were used by Konovalov (1975) to identify stock origins of sockeye salmon; and the brain parasite *Myxobolus arcticus* (previously identified as *M. neurobius*), first reported in sockeye salmon by Bykhovskaya-Pavlovskaya et al. (1962), was important for Konovalov's classification key. The presence of the brain parasite in an individual fish is determined by microscopic examination of prepared brain tissue (Quinn et al., 1987). The percentage of individuals of any sockeye salmon stock infected by this brain parasite (prevalence of the parasite [after Wood et al., 1988]) is quite stable over time and varies from 0% to 100% among samples from stocks in NBA fisheries (Wood et al., 1988; Moles et al., 1990).

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[3] Wishard, L. 1981. Stock identification of Pacific salmon in western Washington using biochemical genetics. Final unpubl. rep., Washington Dep. Fish. Wildl., 300 Desmond Dr., Olympia, WA 98504-7600. Contract nos. 1176 and 1276.

[4] Utter, F., P. Aebersold, J. Helle, and G. Winans. 1984. Genetic characterization of populations in the southeastern range of sockeye salmon. *In* J. M. Walton and D. B. Houston (eds.), Proc. of the Olympic Wild Fish Conference, March 23–25, 1983. [Available from J. M. Walton, Fish. Technol. Prog., Peninsula College, 1502 E. Lauridsen Blvd., Port Angeles, WA 98362.]

Another potentially useful biological character for assessing stock composition of mixed stocks is freshwater age, the number of years young sockeye salmon spend in fresh water before migrating to the ocean. Freshwater age is determined from growth patterns on scales. Individuals of most stocks migrate seaward after spending 1 or 2 yr in fresh water, but freshwater residency can range from 0 to 3 yr (Wood et al., 1988; Rutherford et al., 1994). Freshwater age of individuals of many stocks may be influenced by their growth rates, which vary with changing environmental conditions (Ricker, 1972). Furthermore, spawners of many stocks comprise several ages of maturity (freshwater plus ocean years), each with a distinctive freshwater age composition. As a result, variation in numbers of parent spawners and their (typically) highly variable reproductive success disturb apparent freshwater age composition of their progeny as spawners in annual samples. Therefore, freshwater age composition from annual samples of spawners probably varies more than type composition based on genetic or parasite characters. Wood et al. (1988) suggested that although freshwater age composition of stocks varied among years, the large differences in averages among stocks might yet prove useful for stock composition estimation.

This report describes our assessment of stock composition of sockeye salmon based on four characters: *PGM-1*, PGM-2**, freshwater age, and the presence of *Myxobolus arcticus*. The assessment was applied to catch samples from two Southeast Alaskan fisheries: the purse-seine fishery of area 104 (commonly known as the Noyes Island fishery) in 1986 and a gill-net test fishery in area 106-41 (commonly known as the Sumner Strait fishery) at the northern entrance to Clarence Strait in 1987 (see Fig. 1). During tagging years of 1982 and 1983, significant percentages of catches of both fisheries were Canadian-origin sockeye salmon (Pella et al., 1993). This study describes the utility of the four characters for estimating contributions of U.S.- and Canadian-origin sockeye salmon to these fisheries in years without tagging data and compares the estimates with those from concurrent scale-pattern analysis.

Methods

Samples from the Fisheries

Catches from the two fisheries were sampled weekly during the fishing season. In 1986, a series of eight weekly samples (6 July–30 August) were taken from commercial catches of the Noyes Island purse-seine fishery. In 1987, a series of eight weekly samples (21 June–15 August) were taken from a test gill-net fishery in Sumner Strait that was conducted by personnel of ADF&G to monitor the timing and magnitude of salmon returns for management of the commercial fishery. In both cases, weekly sample size was about 300 fish. Tissue samples (muscle, heart, liver, and eyeball), several lateral scales, and the head were collected from each fish.

According to procedures outlined in Aebersold et al. (1987), fish were typed for *PGM-1** and *PGM-2** from tissue samples. Tissues from the 1986 samples were analyzed at the genetics laboratory of the Coastal Zone and Estuarine Studies Division (CZES) of the NMFS Northwest Fisheries Science Center, and tissues from the 1987 samples were analyzed by the genetics laboratory of ABL. The freshwater age of individuals was determined from examination of scales by staff of the Southeast Alaska Region, Commercial Fisheries Management and Development Division of ADF&G. Brain tissue from the heads was examined for the presence of the parasite *Myxobolus arcticus* at ABL (Moles et al., 1990). Not all characters were measured for each fish sampled. Furthermore, identification of some samples was incomplete, so that collation of all genetic, freshwater age, and parasite information for each individual fish in the sample (as required by the method used to estimate stock composition) was not possible. For fish with incomplete records, only the observed characters identifiable to individual fish were retained for stock composition analysis. Resulting numbers of observations used in assessing stock composition of the catches were substantially reduced, for certain characters and weeks, from the original sample sizes for Noyes Island but not for Sumner Strait (Table 1, 2).

Samples from the Contributing Stocks

Baseline samples (i.e. samples obtained on the spawning grounds of stocks potentially contributing to the catches) of the same four characters were obtained by U.S. and Canadian agencies for 73 sockeye salmon stocks (55 Canadian and 18 Alaskan, Fig. 2). The number of years in which samples were obtained from these baseline stocks was limited, often a single year for a particular character. Most sampling occurred from 1982 to 1986. Collection of baseline samples of all four characters for any stock was not simultaneous, i.e. tissues (two genetic characters), scales (freshwater age), and brain tissue (parasite) were obtained for many stocks at different sampling times. However, tissues for the two genetic characters usually were obtained and assayed, if possible, for each fish in a baseline sample. Genetic analyses were conducted for U.S. stocks at the CZES and ABL genetics laboratories (Helle[5]); and for Cana-

[5] Helle, J. 1992. Auke Bay Laboratory, Alaska Fish. Sci. Center, Natl. Mar. Fish. Serv., NOAA, 11305 Glacier Highway, Juneau, AK 99801. Personal commun.

Table 1

Numbers of sockeye salmon, *Oncorhynchus nerka*, from catch samples by week and character that were used to assess stock composition at Noyes Island in 1986, total fish sampled, and total fishery catches.

	Number of fish					
First day of week	*PGM-1**	*PGM-2**	*Myxobolus arcticus*	Freshwater age	Total samples	Total catch
July 6	230	222	63	45	256	7,192
13	304	299	129	140	313	30,307
20	77	70	184	227	283	53,715
27	280	277	228	219	300	104,325
August 3	258	240	150	201	300	154,415
10	269	275	143	155	298	63,099
17	276	272	107	103	299	15,872
24	274	272	238	240	296	11,989
Totals	1,968	1,927	1,242	1,330	2,345	440,914

Table 2

Numbers of sockeye salmon, *Oncorhynchus nerka*, from catch samples by week and character that were used to assess stock composition at Sumner Strait in 1987, total fish sampled, and total fishery catches.

	Number of fish					
First day of week	*PGM-1**	*PGM-2**	*Myxobolus arcticus*	Freshwater age	Total samples	Total catch
June 21	297	295	298	298	298	3,845
28	293	288	291	294	294	7,514
July 5	299	294	297	299	299	15,175
12	293	290	296	297	297	13,761
19	299	293	300	300	300	14,031
26	294	296	299	299	299	10,232
August 2	292	295	297	297	297	11,075
9	298	295	296	298	298	3,532[1]
Totals	2,365	2,346	2,374	2,382	2,382	79,165

[1] Includes catches for weeks 9 August through 13 September.

dian stocks, at Aqua Life Diagnostics, Ltd., Helix-Biotech, Ltd., and the PBS (Wood[6]). Procedures used were those recommended by Aebersold et al. (1987). Genetic baseline information was reported by Guthrie et al.[7] and Wood et al. (1994). Freshwater ages of fish were determined from scales by staff of ADF&G, PBS, and the Pacific Salmon Commission (PSC). Brain samples were analyzed for presence of *Myxobolus arcticus* by staff of PBS and ABL. Most parasite and freshwater age baseline data from Southeast Alaska and Canada have been published (Wood et al., 1987a, 1988; Moles et al., 1990; Rutherford et al., 1992, 1994). Baseline information used for subsequent analyses is available from the authors upon request.

Estimation of Stock Composition

Maximum-Likelihood Method and Allocate-Sum Procedure—The conditional maximum-likelihood method of estimation of stock composition (Fournier et al., 1984; Millar, 1987; Pella and Milner, 1987) was used to

[6] Wood, C. 1992. Pacific Biological Station, Canada Dep. Fish. and Oceans, Hammond Bay Road, Nanaimo, B.C. Canada V9R 5K6. Personal commun.

[7] Guthrie, C. M., III, J. H. Helle, and A. J. Gharrett. 1994. Genetic relationships among populations of sockeye salmon in Southeast Alaska and northern British Columbia. Auke Bay Laboratory, Alaska Fish. Sci. Center, Natl. Mar. Fish. Serv., NOAA, 11305 Glacier Highway, Juneau, AK 99801. In prep.

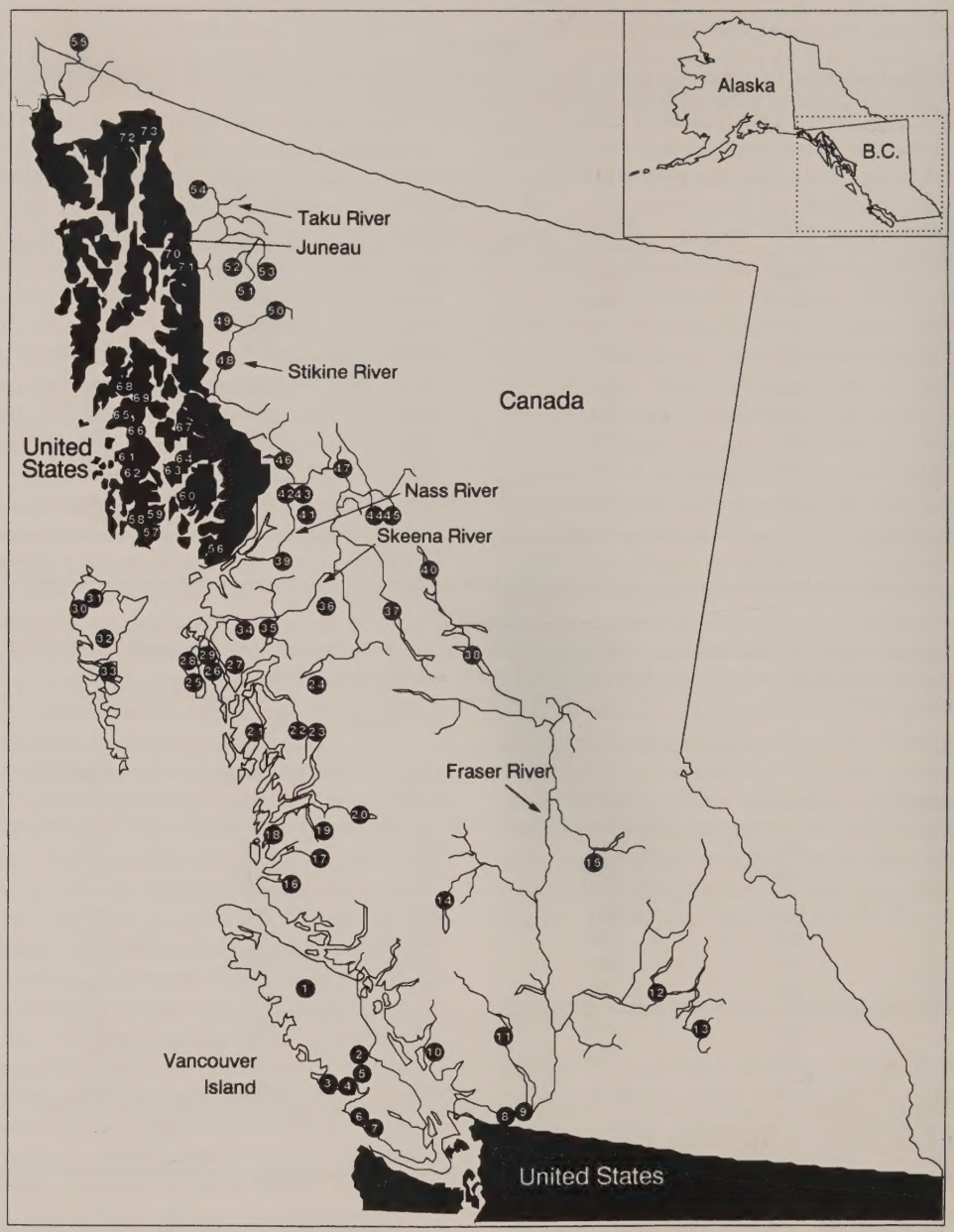

Figure 2
Geographic locations of the 73 sockeye salmon, *Oncorhynchus nerka*, baseline stocks and some of the major rivers (stock reference numbers are defined in Table 3).

estimate percentages of catch samples from each baseline stock. The composite character types of fish in the catch samples were the basis of such an estimation. Conditional stock composition estimates were computed under the assumption that characteristics of baseline stocks were known without error. In addition, the unconditional maximum-likelihood method (Pella and Milner, 1987) was employed for comparison. In unconditional estimation, both stock composition and parameters describing characteristics of baseline stocks were estimated with the optimization begun from the conditional maximum-likelihood estimate of stock composition and observed parameter values for baseline characteristics.

In applying the estimation methods, two common assumptions were made: 1) the genetic loci were in

Hardy-Weinberg equilibrium, and 2) the four characters were mutually independent within the stocks. Hardy-Weinberg equilibrium and independence were expected to be well approximated for the two genetic characters. Any deviations from Hardy-Weinberg equilibrium in a stock would be eliminated in the next generation, provided mate selection was independent of these enzyme genotypes. Genotypes at the two loci are probably inherited independently because linkage has not often been found between enzyme-coding loci in other species of salmonids (Johnson et al., 1987). When such linkages have been found, they are usually present among all species of salmonids examined (Johnson et al., 1987). In particular, breeding experiments found no evidence for linkage between *PGM-1** and *PGM-2** loci for *O. mykiss* (May et al., 1982; Johnson et al., 1987). If the two genetic characters were linked, the disequilibria produced by such linkage would probably have disappeared during the many generations preceding our study (e.g. see discussion on gametic phase disequilibria by Campton [1987]).

The assumption of mutual independence of all characters, including freshwater age and the parasite, is untested. Some evidence (Wood et al., 1987a) indicates that parasite prevalence may increase with length of freshwater residence, at least between the first (0-yr fish) and second summer (1-yr fish); 0-yr fish were a minor component of commercial catches used in this study; therefore this possible dependence would not seriously affect the estimates. Nonetheless, because of concerns regarding the validity of the independence assumption and because of doubts regarding the temporal stability of freshwater age, the analysis was repeated without freshwater age. Regardless of their absolute validity, Hardy-Weinberg equilibrium and mutual independence allow approximations for variables required by the maximum-likelihood method, namely the relative frequencies in each baseline stock of the composite character types observed in catches.

The allocate-sum procedure (Wood et al., 1987b; Wood, 1989) was used to estimate percentages contributed by stocks that were similar in the four characters. Estimated percentages of catch from individual members were summed to obtain the estimated percentages of the similarity group of stocks. Similarity groups were identified from a dendrogram of baseline stock relationships based on Nei's distance (1978) and grouped by the unweighted pair-group method with arithmetic averages (UPGMA) (Sneath and Sokal, 1973).

Numerical Studies—Simulation studies have been recommended for demonstrating that estimates of stock composition are trustworthy because knowledge of the theoretical properties of the method of maximum likelihood is inadequate for credible applications (Fournier et al., 1984; Beacham et al., 1985). Precision and accuracy of our stock composition estimates were examined by means of three numerical studies: bootstrap resampling, local accuracy experiments, and tests of fit.

Bootstrap Resampling—Bootstrap resampling (Efron and Tibshirani, 1986) involved recomputation of stock composition estimates from sets of resampled catch and stock samples. Samples equivalent in size to original samples were drawn with replacement from the original samples. After conditional maximum-likelihood estimates of stock composition were recomputed from each of 100 sets of resampled stock and catch samples, standard deviations of bootstrapped estimates for similarity groups were computed and reported as estimated standard errors of stock composition estimates. For convenience, a stock group is said to be detected if its estimated percentage contribution exceeds two standard errors; however, detection does not invariably indicate stock group presence because of possible confusion among the different groups.

Local Accuracy Experiments—Local accuracy experiments test the capacity of the maximum-likelihood method to detect changes in stock composition of the available mixed-stock samples. If the stock composition of observed mixed-stock samples is altered in a known way, an accurate estimation method should produce estimates that reflect the alteration. Local accuracy engenders credibility in observed stock composition estimates by empirically demonstrating a direct link between underlying stock composition and corresponding expected estimates.

In the local accuracy experiments, the stock composition of each observed catch sample was altered by augmenting it with a computer-generated random sample of equal size and an expected stock composition of equal percentages from the baseline stocks. The computer-generated sample was created by a two-step procedure. First, a multinomial sample with equal expected percentages was drawn for the number of individuals from every baseline stock to be added to the catch sample. Second, the composite type of each individual added to the catch sample was determined by randomly and independently sampling types of each character from the appropriate baseline stock sample. Hardy-Weinberg equilibrium was assumed for relative frequencies of genetic types.

By the experimental process, the unknown stock composition of each original catch sample, $\boldsymbol{p} = (p_1, p_2, \ldots, p_{73})$, was expected to change to that of the augmented sample, $\boldsymbol{p}^*$, as follows:

$$p_i \rightarrow p_i^* = \frac{1}{2}\left[p_i + \frac{1}{73}\right], \; i = 1,2,\ldots,73. \qquad (1)$$

A predicted value for $\boldsymbol{p}^*$ was computed from Equation 1 by substituting components of the original condi-

tional maximum-likelihood estimate ($\hat{\boldsymbol{p}}$) based on observed catch and stock samples for the unknown stock composition ($\boldsymbol{p}$). The baseline samples were resampled, and the conditional maximum-likelihood estimate of stock percentages ($\boldsymbol{p}^*$) for the augmented sample was computed. The process was repeated 100 times. At each repetition, an estimate of the change in stock percentages for an original catch sample, $\hat{\boldsymbol{p}}^* - \hat{\boldsymbol{p}}$, was available for comparison with the single predicted change, $\boldsymbol{p}^* - \hat{\boldsymbol{p}}$. Comparison of estimated and predicted changes in percentages from similarity groups required summing appropriate components of these vectors. Averages of the 100 estimated changes for similarity groups, denoted as $\hat{\Delta}$, and the corresponding predicted change, Δ, were used in further analysis.

Regression analysis was used to compare the average estimated changes of similarity-group percentages in the augmented samples with predicted changes. Let $\hat{\Delta}_{ws}$ be the estimate of change in percentage of similarity group s in the catch sample during week w and let Δ_{ws} be the corresponding predicted change. By separate analysis for the two fisheries, the estimated changes were fitted to the predicted changes by using the linear model

$$\hat{\Delta}_{ws} = \alpha_s + \beta_s \cdot \Delta_{ws} + \varepsilon_{ws}, \tag{2}$$

where α_s and β_s are the intercept and slope, respectively, for the group s line. The simple unweighted least-squares criterion was used in fitting, with the parameter estimates constrained so that

$$\sum_{s=1}^{13} \hat{\alpha}_s = 0 \text{ and}$$
$$\sum_{s=1}^{13} \hat{\beta}_s \cdot \Delta_{ws} = 0,\ w = 1, \ldots, 8. \tag{3}$$

The constraints were a logical consequence of the requirement that fitted values of changes in percentages from similarity groups should sum to zero. Ideally, averages of estimated changes should agree with those that have been predicted, so that expected values of the estimated α's and β's should equal zero and one, respectively.

Tests of Fit—Accurate estimation of stock composition from catch and baseline samples required that 1) stocks present in the catch were included among the baseline stocks and 2) baseline samples and statistical methods provided valid estimates of relative frequencies of composite character types in the baseline stocks. To evaluate the plausibility of these assumptions, the conditional maximum value of the likelihood function for observed catch and baseline samples was compared with an empirical null-reference distribution. The empirical null-reference distribution described variation in the maximum of the likelihood function due to uncertainty in underlying stock composition of the catch, as well as variation induced by sampling the catch and baseline stocks. The following conditions were used in generating the null-reference distribution: 1) catch was composed of baseline stocks only, 2) characters were independent in stocks, 3) relative frequencies of character types within stocks remained stable between times of sampling baseline stocks and catches, and 4) genetic characters were in Hardy-Weinberg equilibrium. Therefore, if the observed conditional maximum value of the likelihood function was unusually small compared with the empirical null distribution, one or more of these conditions were probably not met.

If the true underlying stock composition of a sampled catch was known, the empirical null distribution could be generated by repeating the following steps many times. First, draw a multinomial mixed-stock sample that is equivalent in size to the actual catch sample and that has an expected stock composition equal to the true stock composition. Second, for each individual in the mixed-stock sample, draw a composite character type from the estimated relative-frequency distribution (based on the observed baseline samples) of the appropriate stock to form the simulated catch sample. Third, draw simulated baseline samples of types for each character equivalent in size to and from those available. Fourth, find the conditional maximum of the likelihood function for the simulated catch sample by using the simulated baseline samples to estimate the relative frequencies of its composite character types in the contributing stocks.

The procedure described for generating the null distribution depends on knowledge of the stock composition of the sampled catch. Although the stock composition is unknown, bootstrapped estimates of stock composition provide a measure of uncertainty. To account for this uncertainty in generating the null distribution of the conditional maximum of the likelihood function, the underlying stock composition was set equal to one of the available bootstrapped estimates when generating a set of simulated catch and baseline samples and the derived conditional maximum of the likelihood function. The process was repeated for each of the 100 bootstrapped estimates of stock composition and provided an empirical distribution of 100 values of the conditional maximum of the likelihood function.

Results

Similarities and Differences in Attributes among Baseline Stocks

Observed prevalence of *Myxobolus arcticus* among baseline stocks ranged from complete absence (0%) to complete infection (100%) (Table 3), and the prepon-

Table 3

Similarity groups of sockeye salmon, *Oncorhynchus nerka*, stocks identified from four characters (*PGM-1**, *PGM-2**, *Myxobolus arcticus*, and freshwater age). Stock reference numbers are given as superscripts; Alaskan stocks are identified by *italics*, and percentage of fish parasitized is in parentheses. Cr. = Creek, L. = Lake, R. = River.

Similarity group	Stocks
A	Mikado L.[26] (99)
B	Mercer L.[30] (93)
C	*Shipley L.*[65] (98)
D	Kuthai L.[54] (100), *Speel R.*[70] (87), Damdochax L.[47] (94), Tankeeah L.[19] (100), *Hugh Smith* L.[56] (94), *Chuck L.*[61] (89), *Salmon Bay L.*[69] (96), Eden L.[31] (100), Owikeno L.[17] (99), Banks L.[25] (100), *McDonald L.*[64] (94), *Crescent L.*[71] (98), *Karta R.*[62] (95), Bonilla L.[28] (100), *Luck L.*[66] (98), *Helm L.*[63] (98), Koeye L.[18] (98), Hobiton L.[6] (100), Kennedy L.[3] (99), Swan L.[41] (99), Henderson L.[4] (99), Devon L.[29] (100)
E	*Red Bay L.*[68] (100), *Klakas L.*[58] (100), *Kegan L.*[59] (93)
F	*Thoms L.*[67] (99), *Johnson L.*[57] (100)
G	Canoona L.[21] (100), Cheewhat L.[7] (98), Sproat L.[5] (100), Sakinaw L.[10] (81), Tenas L.[20] (96), Horsefly R.[15] (62)
H	Gingut Cr.[39] (31)
I	Nanika R.[24] (0), *Chilkat L.*[72] (0)
J	Kimsquit L.[23] (0), Motass L.[44] (1), Stikine glacial lakes[49] (7), Tatsamenie L.[51] (0), Bowser L.[46] (0), Meziadin L.[42] (0)
K	Woss L.[1] (55), Mathers L.[33] (30), Lowe L.[27] (41), *Naha R.*[60] (30), Stikine sea/river-type[48] (27)
L	Alastair L.[34] (1), Lakelse L.[35] (3), Hackett R.[53] (3), McDonnell L.[36] (1), Great Central L.[2] (5), Kitlope L.[22] (0), Birkenhead R.[11] (0), *Chilkoot L.*[73] (0), Babine L.[37] (0), Weaver channel[9] (0), Bear L.[45] (0), Trapper L.[52] (0), Yakoun L.[32] (0), Fred Wright L.[43] (2), Cultus L.[8] (0), Tahltan L.[50] (0)
M	Klukshu L.[55] (1), Long L.[16] (0), Takla L.[40] (3), Adams R.[12] (0), Lower Shuswap R.[13] (0), Stuart L.[38] (0), Chilko L.[14] (0)

derance of these stocks (63 of 73 stocks) had either prevalence in excess of 90% (32 stocks, 19 of Canada and 13 of Alaska) or less than 10% (31 stocks, 29 of Canada and 2 of Alaska). The other 10 baseline stocks (7 of Canada and 3 of Alaska) had prevalence ranging from 27% to 89%.

Freshwater age composition of baseline samples varied substantially among stocks (Wood et al., 1987a, 1988; Rutherford et al., 1992, 1994). Many stocks were composed of individuals differing in freshwater residency, most commonly 1- and 2-yr individuals. In most stocks, 1-yr individuals were most frequent, although 2-yr fish predominated in several stocks. Few stocks contained 0- or 3-yr individuals, and the percentages of individuals with these freshwater residence periods were small, with just two exceptions.

The numbers of alleles at the enzyme-coding loci that were detected among the baseline stocks were as follows: *PGM-1**, two alleles; and *PGM-2**, three alleles. *PGM-1** had only two observable phenotypes (one of its two alleles, unlike a normal allele, does not produce a gene product that can be stained and seen), and both occurred commonly in nearly all baseline stocks, albeit in a wide range of relative frequencies among the stocks (Wood et al., 1988; Rutherford et al., 1994). *PGM-2** had six observable genotypes, and each was observed in at least one baseline stock. However, one of the three alleles of *PGM-2** was rare or absent in all stocks. As a result, only three genotypes were common in the baseline stocks for either locus. Nei's (1973, 1977) measure of stock differentiation (GST) was 0.25 for *PGM-1**, 0.11 for *PGM-2**, and 0.19 for both loci.

A dendrogram of baseline stock relationships from the composite characters (*PGM-1**, *PGM-2**, freshwater age, and *Myxobolus arcticus*) (see Fig. 3; Table 3) was truncated on the right side to 13 similarity stock groups labeled A–M. The two major branches of the dendrogram corresponded to high (A–G) and low (H–M) parasite prevalence. The high-prevalence branch (A–G) consisted of 21 Canadian stocks and 15 from Southeast Alaska. The low-prevalence branch consisted of 34 Canadian stocks and 3 from Southeast Alaska.

Stock Composition from Catch Samples

Contributions to the Noyes Island and Sumner Strait fisheries were estimated for each of the 13 stock groups (A, B, ..., M), as well as their consolidations into the high (A–G) and low (H–M) parasite-prevalence branches of the dendrogram.

Catch Samples from Noyes Island, 1986—Combined stocks of the low parasite-prevalence branch (H–M)

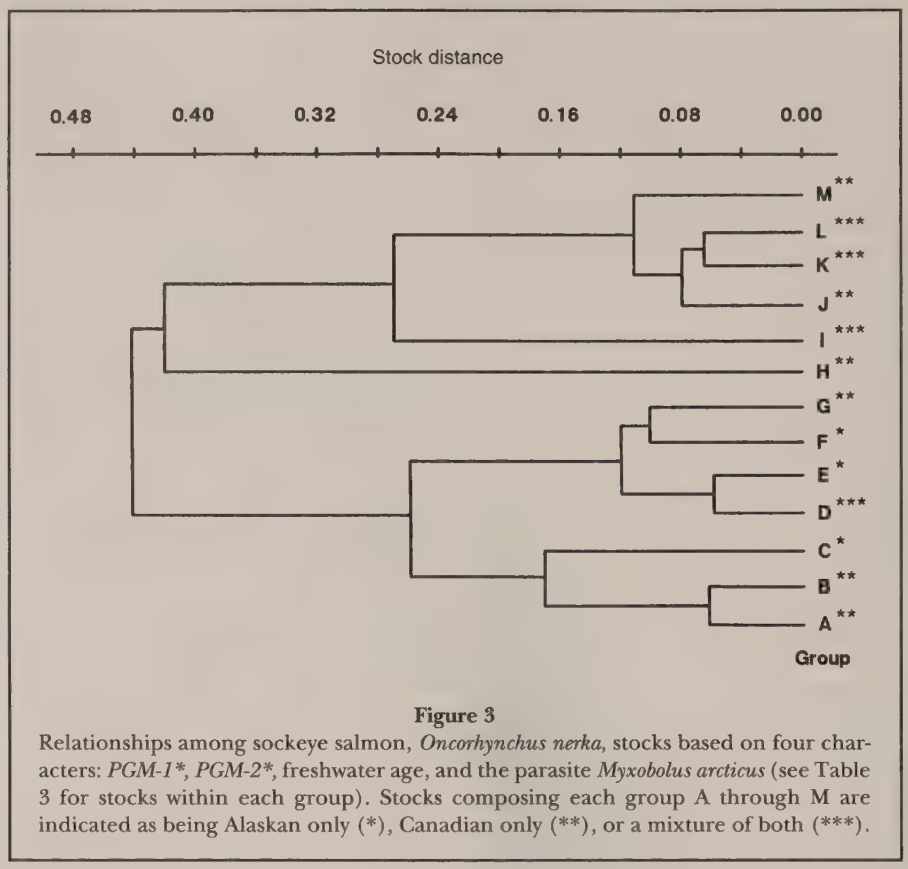

Figure 3

Relationships among sockeye salmon, *Oncorhynchus nerka*, stocks based on four characters: *PGM-1*, PGM-2**, freshwater age, and the parasite *Myxobolus arcticus* (see Table 3 for stocks within each group). Stocks composing each group A through M are indicated as being Alaskan only (*), Canadian only (**), or a mixture of both (***).

were predominant and were detected (detection means the estimated percentage was greater than two standard errors) each week at Noyes Island (Table 4). These stocks were estimated to have contributed 78–92% of weekly catches. The major contributing groups were J, detected in four of eight weeks, and L, detected in seven of eight weeks. In all weeks, either J or L was estimated as providing the greatest percentage of the catches among all groups; in five of eight weeks, estimated percentages from J and L ranked first and second. Other detected groups of the branch were I and M. Group I was detected in two weeks of mid-August. Group M was detected in two of the last three weeks of sampling when its largest estimated contributions occurred.

Combined stocks of the high parasite-prevalence branch (A–G) also were detected each week and were estimated to have contributed 8–22% of the weekly catches. Each of three branch members—groups A, F, and G—was detected in either one or two weeks of the season (Table 4).

Estimated contributions by combined stocks of either parasite-prevalence branch were usually fairly precise with standard errors equaling 3–4% for six of eight weeks (Table 4). Standard errors for estimated contributions by many of their component groups were larger.

Unconditional maximum-likelihood estimates of weekly similarity-group composition at Noyes Island were nearly identical to conditional maximum-likelihood estimates. The largest difference for any week and group was 1.6%. Allowance for change in baseline characteristics only slightly altered perceived stock composition.

Finally, although changes in conditional maximum-likelihood estimates, with omission of freshwater age, were larger among similarity groups within each parasite-prevalence branch, weekly branch totals changed at most by 9.0% and averaged only 2.7% (increase of high parasite-prevalence stocks) over the eight weeks of sampling. For stocks that were detected at Noyes Island from four characters, corresponding estimates from three characters were reasonably well correlated (p=0.77, n=17).

Catch samples from Sumner Strait, 1987—In contrast to Noyes Island, Sumner Strait catches were composed more of stocks of the high parasite-prevalence branch (A–G) (weekly estimates, 50–77%, with average of 66% of catches) than of the low parasite-prevalence branch (H–M) (Table 5). Among groups of the high parasite-prevalence branch , D was consistently abundant (weekly

Table 4

Point estimates (PE) of stock composition (%) of sockeye salmon, *Oncorhynchus nerka*, catches from Noyes Island in 1986 based on two genetic characters (*PGM-1*, PGM-2**), the parasite *Myxobolus arcticus*, and freshwater age. Values are reported by similarity groups from Table 3. Standard errors (SE) are in parentheses. An asterisk(*) indicates group presence was detected (point estimate was greater than two standard errors from zero).

	First day of week							
	6 July		13 July		20 July		27 July	
Similarity group	PE	(SE)	PE	(SE)	PE	(SE)	PE	(SE)
A	0.0	(0.00)	1.5	(2.62)	0.0	(1.40)	3.1	(1.73)
B	0.0	(0.00)	5.5	(3.81)	0.0	(1.37)	0.0	(0.00)
C	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)
D	4.9	(9.08)	1.0	(3.40)	0.1	(2.04)	0.3	(4.34)
E	13.6	(7.75)	1.3	(2.34)	0.1	(3.76)	3.2	(2.40)
F	0.0	(0.00)	9.0*	(4.02)	10.0*	(4.79)	0.0	(0.89)
G	3.9	(2.85)	0.0	(0.88)	9.3	(6.24)	1.3	(1.77)
H	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)
I	18.8	(10.38)	0.0	(4.07)	1.0	(4.47)	6.5	(4.81)
J	21.6	(13.55)	28.0*	(10.54)	34.8*	(12.65)	19.7	(10.45)
K	17.3	(11.86)	12.8	(9.10)	0.0	(3.03)	15.4	(8.37)
L	14.6	(10.15)	37.5*	(10.59)	44.8*	(9.64)	50.4*	(8.88)
M	5.2	(7.38)	3.4	(4.20)	0.0	(3.51)	0.1	(2.21)
A–G	22.4*	(8.20)	18.2*	(3.79)	19.4*	(3.98)	7.8*	(3.19)
H–M	77.6*	(8.20)	81.8*	(3.79)	80.6*	(3.98)	92.2*	(3.19)

	First day of week							
	3 August		10 August		17 August		24 August	
Similarity group	PE	(SE)	PE	(SE)	PE	(SE)	PE	(SE)
A	3.9	(2.46)	0.5	(1.56)	3.8*	(1.86)	2.1	(1.76)
B	0.0	(0.31)	4.6	(2.58)	0.0	(0.16)	0.0	(0.48)
C	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)
D	2.9	(3.12)	2.0	(4.90)	0.0	(0.31)	4.0	(3.96)
E	0.0	(2.22)	3.2	(2.80)	6.3	(3.51)	1.0	(1.43)
F	0.0	(0.99)	0.0	(1.93)	6.3	(3.47)	0.0	(0.48)
G	3.8	(2.86)	5.4	(2.92)	0.0	(1.73)	11.0*	(3.62)
H	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)
I	0.7	(6.01)	16.5*	(6.18)	15.9*	(7.00)	0.7	(2.79)
J	36.9*	(11.93)	13.9	(11.51)	5.8	(11.74)	28.9*	(8.81)
K	1.5	(3.75)	10.4	(7.59)	0.0	(0.02)	10.1	(5.16)
L	50.3*	(8.37)	27.6*	(9.95)	55.4*	(8.08)	23.2*	(9.48)
M	0.0	(3.12)	15.7*	(5.13)	6.5	(5.16)	19.0*	(6.94)
A–G	10.6*	(3.01)	15.7*	(4.62)	16.4*	(3.03)	18.1*	(3.81)
H–M	89.4*	(3.01)	84.3*	(4.62)	83.6*	(3.03)	81.9*	(3.81)

estimates, 11.2–51.6% of catches). Five of its seven groups were detected during the season: A, the last three weeks; D, each week; E, three of the first four weeks; F, five of eight weeks including the first three and last weeks; and G, three weeks of 28 June–4 July, 5 July–11 July, and 26 July–1 August.

The estimated weekly contributions at Sumner Strait from stocks of the low parasite-prevalence branch (H–M) were 24–50% and averaged 34%. Group H was detected each week in small percentages averaging slightly less than 4%. Group I was detected in three weeks including the first and last; J, only in week 19–25 July; K, only in week 26 July–1 August; L, in six of eight weeks; and M, in only the first week (Table 5).

As for Noyes Island, estimated contributions by combined stocks of either parasite-prevalence branch were fairly precise, with standard errors equaling 3–4% for seven of eight weeks (Table 5). Standard errors for estimated contributions by many of their component groups were larger.

Table 5

Point estimates (PE) of stock composition (%) of sockeye salmon, *Oncorhynchus nerka*, catches from Sumner Strait in 1987 based on two genetic characters (*PGM-1* and PGM-2**), the parasite *Myxobolus arcticus*, and freshwater age. Values are reported by similarity groups from Table 3. Standard errors (SE) are in parentheses. An asterisk(*) indicates group presence was detected (point estimate was greater than two standard errors from zero).

	First day of week							
	21 June		28 June		5 July		12 July	
Similarity group	PE	(SE)	PE	(SE)	PE	(SE)	PE	(SE)
A	1.6	(2.29)	1.2	(2.26)	0.0	(1.13)	0.1	(1.88)
B	2.8	(3.39)	0.0	(1.99)	0.0	(1.43)	5.8	(3.62)
C	0.5	(0.49)	0.0	(0.00)	0.5	(0.55)	0.0	(0.00)
D	24.7*	(10.42)	23.1*	(6.89)	11.2*	(5.17)	37.4*	(9.08)
E	33.3*	(9.98)	17.9*	(6.41)	6.3	(4.40)	18.3*	(8.41)
F	13.3*	(6.67)	14.2*	(5.18)	24.0*	(4.88)	4.3	(4.88)
G	0.2	(3.02)	8.1*	(4.09)	7.9*	(2.50)	5.2	(3.26)
H	3.7*	(1.17)	5.8*	(1.51)	3.0*	(1.35)	4.8*	(1.45)
I	3.3*	(1.59)	4.1	(2.53)	4.3	(3.37)	0.0	(1.33)
J	0.1	(2.34)	1.7	(3.58)	6.3	(6.13)	4.4	(2.35)
K	4.0	(3.65)	0.8	(4.40)	5.6	(7.82)	3.5	(4.16)
L	5.3	(3.14)	19.5*	(4.29)	25.9*	(7.38)	11.8*	(3.68)
M	7.2*	(2.79)	3.7	(3.01)	5.2	(3.31)	4.5	(2.49)
A–G	76.5*	(3.83)	64.5*	(3.64)	49.8*	(3.77)	71.1*	(3.12)
H–M	23.5*	(3.83)	35.5*	(3.64)	50.2*	(3.77)	28.9*	(3.12)

	First day of week							
	19 July		26 July		2 August		9 August	
Similarity group	PE	(SE)	PE	(SE)	PE	(SE)	PE	(SE)
A	9.9	(5.80)	14.4*	(6.09)	30.0*	(6.66)	22.6*	(5.56)
B	2.6	(3.19)	1.2	(2.11)	3.1	(3.03)	0.0	(2.16)
C	0.0	(0.00)	0.5	(0.52)	0.5	(0.55)	1.5	(0.92)
D	51.6*	(10.67)	23.3*	(11.48)	23.0*	(9.18)	21.0*	(9.11)
E	0.0	(0.61)	0.0	(2.13)	2.7	(2.98)	1.4	(3.80)
F	4.8	(4.76)	8.3*	(4.01)	3.8	(4.59)	15.4*	(5.35)
G	2.9	(4.63)	13.5*	(5.16)	8.5	(4.53)	1.0	(2.58)
H	1.7*	(0.85)	2.9*	(1.22)	5.1*	(1.48)	3.3*	(1.14)
I	0.7	(1.94)	5.2*	(2.61)	6.0	(3.69)	12.0*	(2.52)
J	9.7*	(3.32)	4.6	(4.68)	6.5	(5.46)	1.1	(3.77)
K	2.3	(5.24)	20.8*	(7.50)	0.1	(2.93)	1.3	(4.84)
L	13.9*	(4.21)	1.7	(4.24)	7.4*	(2.73)	15.2*	(4.32)
M	0.0	(1.58)	3.7	(2.08)	3.0	(1.76)	4.1	(2.22)
A–G	71.7*	(3.87)	61.2*	(5.73)	71.8*	(2.95)	62.9*	(3.57)
H–M	28.3*	(3.87)	38.8*	(5.73)	28.2*	(2.95)	37.1*	(3.57)

The largest difference between unconditional maximum-likelihood estimates of similarity-group percentages and corresponding conditional estimates of any week and group was 3.8%. As with the data from Noyes Island, allowance for change in baseline characteristics only slightly altered perceived stock composition.

Finally, although changes in conditional maximum-likelihood estimates, with omission of freshwater age, were larger among similarity groups within parasite-prevalence branches, weekly branch totals changed at most by 4.6% and averaged 0.6% (increase of high parasite-prevalence stocks) over the eight weeks of sampling.

Local Accuracy Experiments

The purposeful alteration of the stock composition of the Noyes Island and Sumner Strait catch samples was

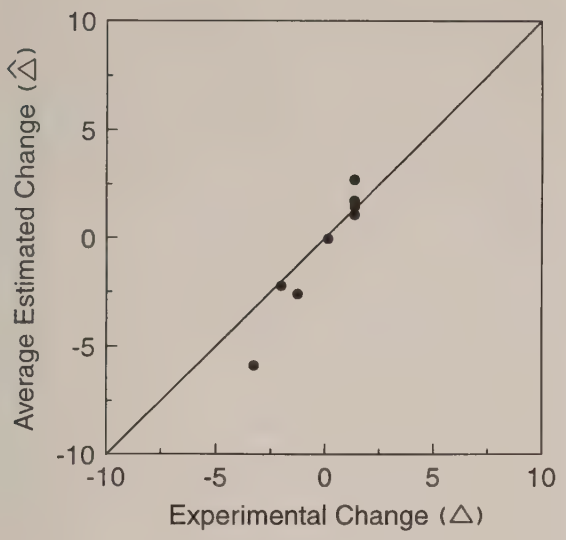

Figure 4
Experimentally induced changes in percentage for similarity group F versus estimated changes by the maximum likelihood method for the eight weekly samples of Noyes Island, 1986.

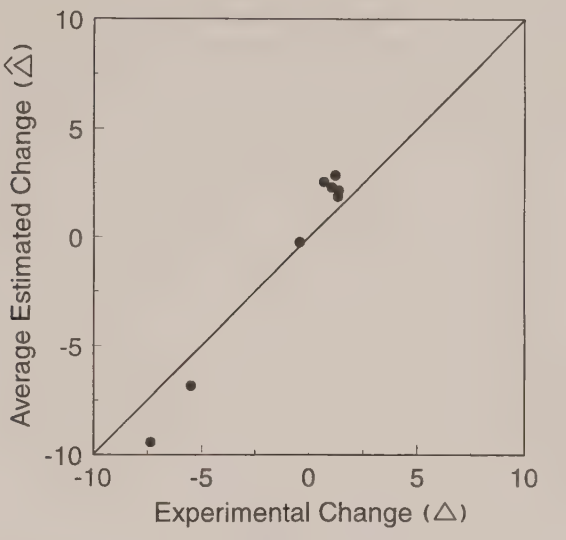

Figure 5
Experimentally induced changes in percentage for similarity group I versus estimated changes by the maximum likelihood method for the eight weekly samples of Noyes Island, 1986.

approximately described by the conditional maximum-likelihood method. Average changes in estimated similarity-group percentages varied roughly in direct relation with our experimentally induced changes (Figs. 4, 5). Most estimated intercepts and slopes for the similarity groups were near zero and unity (Table 6), respectively.

Tests of Fit

Maxima of the logarithm of the likelihood function (support function) computed for weekly Noyes Island samples on the basis of the four characters were far smaller than expected if randomly drawn from the null-reference distribution. However, when freshwater age was omitted, weekly maxima fell nearer to the center of the reference distribution (Table 7). Compared with Noyes Island samples, maxima of the support function for weekly Sumner Strait samples were larger in relation to their null-reference distribution when four characters were included, and omission of freshwater age had a lesser effect on the values (Table 7). All maxima for both sets of weekly samples fell below the 50th percentile when four characters were included, but six of eight maxima (Noyes Island) and eight of eight maxima (Sumner Strait) also fell below the 50th percentile when freshwater age was omitted.

Discussion

Coverage of Contributing Stocks by Baseline Samples

The 73 baseline stocks were distributed from southern British Columbia to northern Southeast Alaska (Fig. 2) and probably accounted for most fish in NBA catches. Most large Canadian and Alaskan stocks of sockeye salmon that contributed to NBA fisheries were included in the baseline. The baseline comprised stocks of the major Canadian rivers: Nass River, Skeena River, and Fraser River. Two of these Canadian stocks were that from Babine Lake in the Skeena River (Group L, Table 3) and that from Meziadin Lake of the Nass River (Group J), both known from tagging studies to occur abundantly at Noyes Island and to a lesser degree at Sumner Strait (Pella et al., 1993; Gazey et al.[1]; English et al.[2]). The tagging studies also showed that stocks of the Fraser River, some of which were very abundant, contributed measurably to catches at Noyes Island in late season (Pella et al., 1993; English et al.[2]). Nine Fraser River stocks were in the baseline, including four of its largest populations during the catch sampling years of 1986 and 1987: Birkenhead River stock (Group L); and Adams River, Chilko Lake, and Lower Shuswap River stocks (Group M). Finally, the largest sockeye salmon stocks of the British Columbia central coast were three

Table 6

Estimates of similarity group intercept (α_s) and slope (β_s) and their estimated standard errors (SE) from local accuracy experiments for Noyes Island and Sumner Strait samples (NA = not available).

Similarity group	$\hat{\alpha}_s$	SE($\hat{\alpha}_s$)	$\hat{\beta}_s$	SE($\hat{\beta}_s$)
Noyes Island				
A	0.2	0.76	1.1	0.89
B	–0.0	0.68	1.2	0.54
C	NA	NA	NA	NA
D	11.3	10.02	0.2	0.69
E	–0.5	0.67	1.8	0.31
F	–0.3	0.67	1.5	0.39
G	0.4	0.75	1.4	0.30
H	NA	NA	NA	NA
I	0.7	0.70	1.4	0.21
J	3.9	1.31	1.6	0.11
K	2.0	0.67	1.3	0.20
L	0.7	0.92	1.4	0.09
M	1.1	0.72	1.1	0.19
Sumner Strait				
A	0.1	0.58	1.1	0.08
B	–0.1	0.47	0.9	0.47
C	0.0	1.02	1.0	1.98
D	0.5	0.47	1.1	0.08
E	0.1	0.51	1.1	0.08
F	–0.9	0.72	0.9	0.14
G	0.5	0.51	1.1	0.21
H	0.0	0.96	0.9	0.70
I	–0.3	0.50	1.1	0.26
J	0.2	0.74	1.3	0.30
K	–0.7	0.47	1.5	0.14
L	–2.5	0.73	1.3	0.12
M	0.8	1.41	1.0	0.47

Table 7

Percentiles of the null-reference distributions for conditional maxima of the logarithm of the likelihood function computed from Noyes Island and Sumner Strait weekly samples of sockeye salmon, *Oncorhynchus nerka*, based on 1) all four characters: *PGM-1*, PGM-2*, Myxobolus arcticus*, and freshwater age, and 2) three of the four characters (freshwater age was omitted).

First day of week		Percentile of null-reference distribution: 4 characters	3 characters
Noyes Island			
July	6	2	34
	13	1	38
	20	1	33
	27	3	58
August	3	1	50
	10	1	39
	17	1	36
	24	1	49
Sumner Strait			
June	21	33	38
	28	11	25
July	5	14	21
	12	18	24
	19	28	45
	26	22	44
August	2	19	41
	9	31	43

baseline stocks: Owikeno Lake stock (Group D), Tenas Lake stock (Group G), and Long Lake stock (Group M).

Baseline stocks accounted for a substantial portion of sockeye salmon from Southeast Alaska. Most (14 of 18 stocks) Southeast Alaskan baseline stocks were from southern Southeast Alaska because tagging studies supported conjectures that northern Southeast Alaskan stocks ordinarily contributed only minor numbers to NBA fisheries (Pella et al., 1993). Nonetheless, four stocks of northern Southeast Alaska were included in the baseline. Two northern Southeast Alaskan baseline stocks, those of Chilkat (Group I, Table 3) and Chilkoot (Group L) Lakes, are among the largest sockeye salmon populations in all of Southeast Alaska (McPherson, 1990). Only about one-fourth of the known number of southern Southeast Alaskan stocks (14 of 59) were baseline stocks; however, these baseline stocks composed a much larger portion of the combined populations from this region. Nine of the 12 largest stocks of southern Southeast Alaska were included in the baseline: Hugh Smith Lake, McDonald Lake, Salmon Bay Lake, Karta River, and Luck Lake stocks (Group D); Klakas Lake and Kegan Lake stocks (Group E); Thoms Lake stock (Group F); and Naha River stock (Group K). Combined weir counts and peak foot-survey counts of southern Southeast Alaskan baseline stocks during the tagging years of 1982 and 1983 equaled 42% (1982) and 47% (1983) of this region's estimated total escapements (325,000–350,000 fish, Pella et al., 1988). Although many Southeast Alaskan stocks were not included in the baseline, one of their attributes—parasite prevalence—could be inferred from the similarities and differences of available baseline samples and was valuable in assessing contributions of Alaskan and Canadian stocks to NBA fisheries.

Similarities and Differences in Attributes among Baseline Stocks

Percentages of NBA catches from stock groups (H–M) of the low parasite-prevalence branch could be consid-

ered almost entirely of Canadian origin if northern Southeast Alaskan stocks were always negligible contributors as they were in the tagging years of 1982 and 1983. Baseline stocks of the low-prevalence branch were predominantly from Canada; 34 stocks were Canadian and only 3 were Alaskan. Among the latter, 2 were from Chilkat and Chilkoot Lakes in northern Southeast Alaska; the third stock was from Naha River in southern Southeast Alaska. All 15 other baseline stocks of Southeast Alaska (2 of 4 baseline stocks from northern Southeast Alaska and 13 of 14 baseline stocks from southern Southeast Alaska) had parasite prevalence of 87–100% and belonged to the high parasite-prevalence branch (Table 3).

Although individuals in NBA catches from stocks belonging to the low parasite-prevalence branch were probably mainly of Canadian origin, the country of origin of fish from stocks of the high parasite-prevalence branch was unclear: 21 of these baseline stocks were Canadian and 15 were Alaskan. Although stocks with high parasite prevalence were preponderant in Southeast Alaska, they were common to Canada as well, making it difficult to identify the country of origin for individuals in NBA catches belonging to this branch. On the other hand, such estimates reasonably provide upper bounds for highly parasitized Alaskan stocks in catches.

Stock Composition from Catch Samples

Notwithstanding statistical imprecision, estimated contributions to the Noyes Island and Sumner Strait fisheries by certain groups comprising major stocks were roughly consistent with background knowledge of population magnitudes and migration routes. However, apparent presence (indicated by statistical detection) of some groups composed of lesser stocks disagreed with expectations at times. Additional aggregation of the 13 stock groups into consolidations of low and high parasite-prevalence branches was of practical interest because of the apparent predominance of Canadian fish among stock groups of the low-prevalence branch and because of the improved precision of such estimates. The accuracy of estimated contributions by combined groups of major stocks of the large Canadian rivers was supported by comparison with independent ADF&G assessments in which scales were used.

Catch Samples from Noyes Island, 1986—Canadian stocks were chief contributors to catches at Noyes Island. Stocks of the low parasite-prevalence branch (Groups H–M), composed mainly of Canadian stocks, preponderated in all weekly catches; and stocks of the high parasite-prevalence branch (Groups A–G), a mixture of stocks from Canada and Alaska, contributed the rest. The major contributing groups, J and L, were expected to be well represented at Noyes Island throughout the season because of relatively large escapements among NBA stocks to Meziadin Lake (Group J) and Babine Lake (Group L) (Pella et al., 1988; Pacific Salmon Commission[8,9]) and the predominance of these two stocks at Noyes Island during the tagging experiments of 1982 and 1983 (Pella et al., 1993; Gazey et al.[1]; English et al.[2]). Estimates of stock composition at Noyes Island from tagging (Pella et al., 1993) indicated that over 60% of the 1982 and 1983 catches were from the Skeena River, mainly the Babine Lake stock, and over 10% were from the Nass River, mainly the Meziadin Lake stock. During both tagging years, the estimated percentage contributed by the Babine Lake stock to Noyes Island catches during the last half of July reached 80–90%. Escapements to the Skeena River declined in 1986 to 0.7 million sockeye salmon from escapements of 1.2 million and 0.9 million fish in 1982 and 1983, respectively (Pacific Salmon Commission[9]). Escapements to the Nass River, another major contributor at Noyes Island in 1982 and 1983, also declined slightly in 1986 to 0.2 million sockeye salmon from escapements of 0.3 million and 0.2 million fish in 1982 and 1983, respectively (Pacific Salmon Commission[9]).

Independent evidence for presence of group M, comprising large Fraser River stocks, was provided by Pacific Salmon Commission catch samples from Noyes Island. Scale features of the sampled fish and their length and age composition indicated that Fraser River fish were at Noyes Island during the last four weeks and were most abundant in the last two weeks (Woodey[10]). This time of appearance coincided with our detection of group M in two of the last three weeks when largest estimated contributions occurred. Fraser River stocks were very large compared with other contributors in 1986 with 3.7 million total escapement, including that of baseline Adams River (1.3 million escapement) and Lower Shuswap River stocks (0.6 million escapement) (Pacific Salmon Commission[8]). Over 50% of the estimated total return of 16 million fish to the Fraser River in 1986 was from the Adams River and Lower Shuswap River stocks (Pacific Salmon Commission[8]).

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[8] Pacific Salmon Commission. 1988. Report of the Fraser River Panel to the Pacific Salmon Commission on the 1986 Fraser River sockeye salmon fishing season, 36 p. Pacific Salmon Commission, 600-1155 Robson St., Vancouver, B.C., Canada V6E 1B5.

[9] Pacific Salmon Commission. 1992. Northern Boundary Technical Committee Report. U.S./Canada northern boundary area. 1992 salmon fisheries management report and 1993 preliminary expectations. Report TCNB(92)-1, 160 p. Pacific Salmon Commission, 600-1155 Robson St., Vancouver, B.C., Canada V6E 1B5.

[10] Woodey, J. 1994. Pacific Salmon Commission, 600-1155 Robson St., Vancouver, B.C. Canada V6E 1B5. Personal commun.

During mid-August, the Alaskan Chilkat Lake and Canadian Nanika River stocks, composing group I, were likely mistaken for abundant and similar stock groups such as J and L. Historically, sockeye salmon of the Nanika River stock have passed through terminal fishing areas between late June and late July (Jantz[11]); in 1986, fish of the Chilkat Lake stock continued through the weir from early July to the end of September (McPherson, 1990). The 1986 Nanika River escapement count was 3,000 (Peacock[12]), compared with the Chilkat Lake escapement count (weir count) of about 24,000 (McPherson, 1990). Considering the small size of the Nanika River stock and its migration through the fisheries before detection of the group during mid-August, the fish at Noyes Island were more likely from Chilkat Lake if they were from either of the two stocks. Substantial numbers of Chilkat Lake sockeye salmon were not expected at Noyes Island in 1986 based on results of the tagging programs of 1982 and 1983.

Group A of the high parasite-prevalence branch, the Canadian Mikado Lake stock, was detected as contributing less than 4% in the week 17–23 August. This small stock (1986 escapement count: 2,000) was expected to migrate through terminal fishing areas by mid-July (Jantz[11]), therefore another contributing group was presumably mistaken for Group A.

Group G of the high parasite-prevalence branch, composed of Canadian stocks ranging from the Fraser River to the Canadian central coast, was detected in only the last week. Catches at Noyes Island during at least the last three weeks probably contained a broad mixture of stocks from Alaska southward to the Fraser River.

Catch Samples from Sumner Strait, 1987—In contrast to Noyes Island, stocks of the high parasite-prevalence branch (Groups A–G), rather than the low parasite-prevalence branch (Groups H–M), were more abundant at Sumner Strait. The five detected groups of this branch (A, D, E, F, and G) included Alaskan and Canadian stocks. Each stock group of the less-abundant, low parasite-prevalence branch (Groups H–M), composed mainly of Canadian stocks, was detected at Sumner Strait sometime during sampling.

Significant contributions to catches at Sumner Strait were expected from stocks of southern Southeast Alaska (included in groups D, E, F, and K), Nass River (Meziadin Lake stock of Group J), Skeena River (Babine Lake stock of Group L), and Stikine River (Tahltan Lake stock of Group L), based on geographical locations of the fishery and spawning grounds, magnitudes of stocks, and results of tagging experiments on returning adults (Pella et al., 1993; Gazey et al.[1]; English et al.[2]). Group D contained many of the largest stocks of southern Southeast Alaska, including the large McDonald Lake stock, known from the coded-wire tagging of outmigrant smolts to return as adults predominantly by means of Sumner Strait (Van Alen[13]).

Adult sockeye salmon were tagged in Sumner Strait during the 1983 fishing season (Pella et al., 1993; English et al.[2]), and computed stock composition indicated that Alaskan stocks contributed 49% of the catch; nearly all the remainder was from Nass River (15%), Skeena River (20%), and Stikine River stocks (15%). Escapements to the Skeena River increased to 1.3 million sockeye salmon in 1987 from 0.9 million in 1983 (Pacific Salmon Commission[9]). Escapements to the Nass River in 1987 equaled 0.2 million sockeye salmon, essentially unchanged from 1983 (Pacific Salmon Commission[9]). Escapements to southern Southeast Alaska in 1987 were unknown but were estimated at 0.3 million sockeye salmon in 1983 (Pella et al., 1988).

Other stock groups, including A, H, I, and M, were detected at times in Sumner Strait, but their actual presence is doubtful. More likely, fish of other stock groups were confused with those of these groups. Group A, the Canadian Mikado Lake stock, was detected in apparent abundance (14.4–30.0%) during the last three weeks and after its expected migration through the NBA fisheries (Jantz[11]).

The apparent persistence of Group H, the Gingut Creek stock, throughout the season was caused by the small and continual occurrence (1.7–5.8%; average, 3.9%) of age-0 fish in the weekly test-fishery samples and their scarce presence in baseline samples. Other sockeye salmon populations, composed mainly of age-0 fish, are also known to spawn in the lower Nass River system, of which Gingut Creek probably supports the largest numbers (Rutherford et al., 1994). Nonetheless, the Gingut Creek stock is usually small and had an escapement count of only 1,000 fish in 1987 (Peacock[12]). Time of return of the lower Nass River stocks through terminal fisheries probably occurs from early June to the first week of July (Rutherford et al., 1994; Jantz[11]). Therefore, these stocks were probably not present in Sumner Strait for at least the last five weeks. More likely, either the baseline percentages of age-0 fish in some baseline stocks present in Sumner Strait during 1987 were too low because freshwater age composition changed after the time of baseline sampling or stocks present at Sumner Strait with higher percentages of age-0 fish were not included in the baseline. In particular, higher percentages (up to 44%) of freshwater age-0

[11] Jantz, L. 1992. Canada Dep. Fish. and Oceans. 202-417 2nd Ave. W., Prince Rupert, B.C., Canada V8J 1G8. Personal commun.

[12] Peacock, D. 1992. Canada Dep. Fish. and Oceans, 202-417 2nd Ave. W., Prince Rupert, B.C., Canada V8J 1G8. Personal commun.

[13] Van Alen, B. 1993. Alaska Dep. Fish and Game, P.O. Box 240020, Douglas, AK 99824-0020. Personal commun.

fish have been found at some locations within the Stikine River drainage (Wood et al., 1987a).

Again, fish of similar stocks present at Sumner Strait probably were misassigned to Group I (Chilkat Lake and Nanika River stocks). The largest contribution detected (12.0%) occurred during the last week, 9–15 August, after Nanika River fish had presumably passed through terminal fisheries (Jantz[11]). Escapement to Chilkat Lake was about 49,000 fish in 1987 (McPherson, 1990) and occurred from late June to the end of September. The escapement count to Nanika River was 4,000 (Peacock[12]). The Chilkat Lake stock was not expected to be present in substantial numbers if their migration was like that during the 1982 and 1983 tagging experiments.

Finally, fish of similar stocks were probably misassigned to Group M. No sockeye salmon tagged in Sumner Strait or Clarence Strait (adjoining Sumner Strait) during the 1982 or 1983 studies were recovered from southern Canadian fisheries or escapements. If Fraser River stocks were present at Sumner Strait in 1987, migration routes must have changed since the tagging years.

Comparison of Stock Composition Estimates with Those Based on ADF&G Scale Pattern Analysis

Weekly scale samples from the 1986 Noyes Island commercial purse-seine catches and the 1987 Sumner Strait commercial gill-net catches (recall that our samples were obtained from the Sumner Strait test gill-net fishery) were classified to stock groups by linear discriminant functions and used to estimate stock group percentages in the weekly catches (Jensen and Frank, 1988; Oliver et al.[14]). Classification functions were developed for each of the four significant age groups of sockeye salmon (1.2, 1.3, 2.2, and 2.3) occurring in either fishery, by using scale characters observed in baseline samples of the appropriate year of return. For the Noyes Island analysis, baseline scale samples were aggregated into four stock groups: 1) Nass River, 2) Skeena River, 3) Alaskan stocks typified by McDonald Lake of Southeast Alaska, and 4) other Southeast Alaskan stocks. Fraser River stocks, now thought to have been present at Noyes Island late in the season of 1986, were not included in the scale baseline. The Pacific Salmon Commission[8] estimated 12,000 (2.7%) of 445,000 sockeye salmon caught at Noyes Island were from the approximately 16 million Fraser River return of 1986. For the Sumner Strait analysis, baseline scale samples were assembled into five groups of stocks: 1) Alaska I, typified by Salmon Bay Lake and Hugh Smith Lake patterns; 2) Alaska II, typified by the McDonald Lake pattern; 3) Nass River and Skeena River; 4) Stikine River; and the 5) Tahltan Lake stock of the upper Stikine River.

As noted earlier, scales of stocks from spawning grounds in interior British Columbia within the Nass River, Skeena River, and Fraser River differ from scales of coastal stocks. Misclassification of scales among stocks of the major Canadian rivers is more likely than between those Canadian stocks and Southeast Alaskan stocks. Similarly, our method more likely misassigns contributions among stocks within the high and low parasite-prevalence branches of the dendrogram than between these branches. If stocks of the J, L, and M groups of the low parasite-prevalence branch other than those of the Nass, Skeena, and Fraser Rivers were minor contributors to the catches, classification by scales may well have assigned most fish of these three groups as either of Nass or Skeena River origin. If so, the sum of Nass and Skeena River percentages based on scales should agree with the sum of percentages from groups J, L, and M, based on *PGM-1**, *PGM-2**, freshwater age, and *Myxobolus arcticus* (Fig. 6). Agreement was only fair among weeks of the season at Noyes Island (p=0.37 with

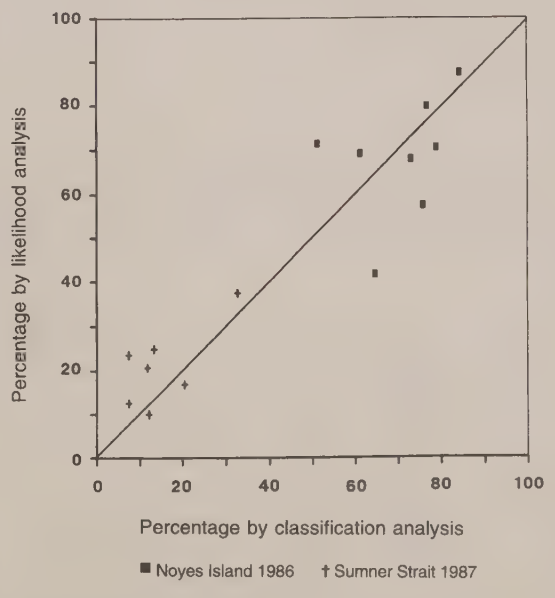

Figure 6

Comparison of weekly point estimates of percentages of catches of sockeye salmon, *Oncorhynchus nerka*, at Noyes Island in 1986 and Sumner Strait in 1987 from stock groups J, L, and M (likelihood analysis based on *PGM-1**, *PGM-2**, *Myxobolus arcticus*, and freshwater age) and Nass and Skeena River stocks (classification analysis based on scales).

[14] Oliver, G. T., K. A. Jensen, I. S. Frank, and N. J. Sands. 1987. Contribution of Alaskan, Canadian, and transboundary sockeye stocks to catches from Southeast Alaskan districts 101–108, 1986, based on analysis of scale patterns. Unpubl. rep., 39 p. Alaska Dep. Fish and Game, Div. Commer. Fish., Douglas, AK 99824.

n=8) and Sumner Strait (p=0.69 with n=7). However, by combining pairs of estimates by the two methods from Noyes Island and Sumner Strait into a single sample, good overall agreement was evident (p=0.92 with n=15). Clearly, both approaches detected fish of the same stock groups as expected. However, sampling errors and possible contributions from stocks other than those of the Nass River, Skeena River, and Fraser River to the J, L, and M similarity groups were disruptive. When the difference in total percentage contributed by Canadian interior stocks was large, as between Noyes Island and Sumner Strait, both approaches discovered the change.

Although assessments of stock percentages from the large Canadian rivers agreed fairly well between methods, a persistent discrepancy was evident between the parasite prevalence in catch samples and the estimates of Alaskan contributions to the Noyes Island and Sumner Strait catches based on classification from scales. The scale and parasite samples were collected under different sampling schedules; scale samples were larger and represented the fishing fleets better. In particular, parasite samples at Noyes Island may have emphasized catches from the southern portion of the fishery, owing to practical constraints (Van Alen[13]), and the Sumner Strait parasite samples were from the test fishery rather than the commercial fishery. On the other hand, if the parasite samples were representative of the parasite prevalence in the catches in either fishery, some scales from high parasite-prevalence Alaskan stocks in the scale baselines must have been similar to those of low parasite-prevalence stocks omitted from the scale baselines. These low parasite-prevalence stocks were probably from Canada; if not, then they were almost surely from northern Southeast Alaska because 13 of 14 stocks from southern Southeast Alaska, including most of the larger stocks, were highly parasitized (Table 3). If results of the 1982 and 1983 tagging studies apply, fewer northern Southeast Alaskan sockeye salmon would be expected at Sumner Strait than at Noyes Island; and in neither fishery were large numbers of northern Southeast Alaskan sockeye salmon expected (Pella et al., 1993).

If all the parasitized fish in catches at Noyes Island and Sumner Strait were from Alaskan stocks, an estimate of the percentage of Alaskan fish that were parasitized could be obtained by dividing the percentage of parasitized fish in the samples by the estimated percentage of catch from Alaska based on scales (Tables 8, 9). At Noyes Island (Table 8), only the improbable presence of large numbers of fish from low parasite-prevalence Alaskan stocks, like the large stocks of Chilkat Lake and Chilkoot Lake from northern Southeast Alaska, could account for the apparently low percentage of Alaskan fish that were parasitized. Unweighted

Table 8

Comparison of observed parasite, *Myxobolus arcticus*, prevalence of the 1986 sockeye salmon, *Oncorhynchus nerka*, samples from Noyes Island purse-seine catches, percentage of catch judged from scales to be of Alaskan origin, parasite prevalence of Alaskan fish if all parasitized fish were Alaskan, and implied minimum percent contribution from low-parasitized Alaskan stocks such as (1) Chilkat Lake and Chilkoot Lake or (2) Naha River.

	First day of week							
	6 Jul	13 Jul	20 Jul	27 Jul	3 Aug	10 Aug	17 Aug	24 Aug
Percent with parasite[1]	34	25	20	15	13	22	18	23
Percent Alaskan by scales[2]	36	39	24	21	16	24	27	49
Percent Alaskan with parasite[3]	96	64	85	70	81	90	66	47
Implied minimum percent from								
1) Chilkat Lake and Chilkoot Lake[4]	–4	30	8	24	12	2	28	49
2) Naha River[5]	0	48	17	39	23	9	45	74

[1] Source: Moles et al. (1990).

[2] Source: Oliver et al.[14].

[3] Computed as 100 × percent with *Myxobolus arcticus* ÷ percent Alaskan by scales, i.e., assuming all parasitized fish were from Alaska.

[4] Percent Chilkat Lake and Chilkoot Lake stocks ($p \times 100\%$) satisfies the mixture equation relating prevalence of the parasite among Alaskan sockeye salmon in the catch samples (λ) with prevalence in Chilkat Lake and Chilkoot Lake stocks (0%) and average prevalence among the other Alaskan stocks (92%), i.e. $p \times 0\% + (1 - p) \times 92\% = \lambda$.

[5] Percent Naha River stock ($p \times 100\%$) satisfies the mixture equation relating prevalence of the parasite among Alaskan sockeye salmon in the catch samples (λ) with prevalence in the Naha River stock (30%) and average prevalence among the other Alaskan stocks (96%), i.e. $p \times 30\% + (1 - p) \times 96\% = \lambda$.

average prevalence of the parasite among the 14 baseline stocks of southern Southeast Alaska was 92%; if parasite prevalence of stocks could be weighted by magnitude of return (annual information is not available for most stocks), the weighted average would probably be even higher because the largest stocks have high parasite prevalence. If the parasitized fish of catches were composed of a mixture of Chilkat Lake and Chilkoot Lake fish (0% prevalence) and fish of other Alaskan stocks (92% prevalence), the Chilkat Lake and Chilkoot Lake stocks must have contributed between 0 and 49% of the Noyes Island weekly catches, with average contribution of 19% (Table 8). Unless migration routes of sockeye salmon in 1986 were radically different from those during the tagging years of 1982 and 1983, Chilkat Lake and Chilkoot Lake fish would not be present in such abundance, and thus the estimates of percentage of catches from Alaskan stocks based on scales appear too high if estimated parasite prevalence was representative of commercial catches. If an abundance-weighted rather than unweighted average of the parasite prevalence among Southeast Alaskan fish had been used in the computations or if some parasitized fish in Noyes Island catches were from Canadian stocks (as seems certain because Canada also has numerous heavily parasitized stocks), the necessary contributions by low parasite-prevalence Alaskan stocks, such as those of Chilkat Lake and Chilkoot Lake, would be even greater.

As for Noyes Island, estimated weekly percentages of Alaskan fish in Sumner Strait that were parasitized appeared unreasonably low in most weeks when calculated from parasite prevalence of our test-fishery catch samples and from stock composition of commercial gill-net catches determined from scales (Table 9). Average prevalence of the parasite among the 13 baseline stocks of southern Southeast Alaska, excluding Naha River stock, was 96%; Naha River stock had 30% prevalence. If the parasitized Alaskan fish comprised a mixture of the Naha River (30% prevalence) and other southern Southeast Alaskan stocks (96% prevalence), the Naha River stock must have contributed 17–23% of the Sumner Strait catch over the first six weeks (Table 9). Unless abundance of the Naha River stock greatly increased from 1983, when the bulk of escapement through a weir was roughly 5,000 fish (Pella et al., 1988), such a significant contribution is implausible. In 1983, tagging studies indicated that all stocks of Alaskan district 101 (including the Naha River stock and larger stocks of McDonald Lake and Hugh Smith Lake) contributed less than 30% to the Sumner Strait catch (Pella et al., 1993). Because the omission from the baseline of significant, low parasite-prevalence, southern Southeast Alaskan stocks is unlikely, estimates of the percentage of Sumner Strait catches from Alaskan stocks based on scales also appear too high without the significant presence of low parasite-prevalence Alaskan stocks like Chilkat Lake and Chilkoot Lake (Table 9).

Table 9

Comparison of observed parasite, *Myxobolus arcticus*, prevalence of the 1987 sockeye salmon, *Oncorhynchus nerka*, test fishery samples from Sumner Strait, percentage of fishery samples judged from scales to be of Alaskan origin, parasite prevalence of Alaskan fish if all parasitized fish were Alaskan, and implied minimum percent contribution from low-parasitized Alaskan stocks such as (1) Chilkat Lake and Chilkoot Lake or (2) Naha River.

	First day of week							
	21 Jun	28 Jun	5 Jul	12 Jul	19 Jul	26 Jul	2 Aug	9 Aug
Percent with parasite[1]	78	69	54	74	73	73	75	65
Percent Alaskan by scales[2]	91	86	62	87	90	88	80	—
Percent Alaskan with parasite[3]	85	81	87	85	81	83	94	—
Implied minimum percent from								
1) Chilkat Lake & Chilkoot Lake[4]	8	12	5	8	12	10	–2	—
2) Naha River[5]	17	23	14	17	23	20	3	—

[1] Source: Moles et al. (1990).

[2] Source: Jensen and Frank (1988).

[3] Computed as 100 × percent with *Myxobolus arcticus* ÷ percent Alaskan by scales, i.e., assuming all parasitized fish were from Alaska.

[4] Percent Chilkat Lake and Chilkoot Lake stocks ($p \times 100\%$) satisfies the mixture equation relating prevalence of the parasite among Alaskan sockeye salmon in the catch samples (λ) with prevalence in the Chilkat Lake and Chilkoot Lake stocks (0%) and average prevalence among the other Alaskan stocks (92%), i.e. $p \times 0\% + (1 - p) \times 92\% = \lambda$.

[5] Percent Naha River stock ($p \times 100\%$) satisfies the mixture equation relating prevalence of the parasite among Alaskan sockeye salmon in the catch samples (λ) with prevalence in the Naha River stock (30%) and average prevalence among the other Alaskan stocks (96%), i.e. $p \times 30\% + (1 - p) \times 96\% = \lambda$.

Local Accuracy Experiments

The conditional maximum-likelihood method was capable of quantitatively assessing the experimentally induced changes in stock composition of mixed-stock samples with available sample sizes from stocks and weekly catches. Although available sample sizes were adequate for the purpose of discovering and describing changes in contributions from similarity groups A–M under local accuracy experimental conditions, the potential variation in estimated similarity-group percentages from the available samples was often large unless similarity groups were further consolidated into high and low parasite-prevalence branches of the dendrogram (Tables 4, 5).

Local accuracy was demonstrated when composite types of individuals of the computer-generated sample (appended to the actual catch sample) were assigned by reference to the baseline samples. However, relative frequencies of genotypes in the baseline stocks must have varied among years from genetic drift alone, especially for small populations (Crow and Kimura, 1970). Relative frequencies of types for the nongenetic characters—parasite prevalence and especially freshwater age—probably varied even more than for genetic characters (Wood et al., 1988). Occurrence of such variations between times of sampling baseline stocks and catches was investigated by tests of fit.

Tests of Fit

Variation in relative frequencies of character types within stocks, especially of freshwater age, between the sampling times of stocks and catches was probably responsible for the discernible lack of fit of the mixed-stock model. The fit of the model, with freshwater age omitted, was improved: nonetheless, other conditions used to generate the null distribution may not have been realized in actual sampling. Certainly, some drift in relative frequencies of genotypes between baseline and catch sampling may have occurred, and stocks absent from the baseline may have been present in the catches.

Summary

Sockeye salmon caught in NBA fisheries, including Noyes Island and Sumner Strait, comprise mixtures of Canadian and Alaskan stocks. Annual variations in numbers of salmon returning to stocks and in the migration routes of these salmon through the NBA make estimation of stock composition in fisheries imprecise without regular monitoring of catches for stock composition. At present, scales from fish in catch samples are used in the monitoring of these stocks. Scale features vary among years; therefore baseline samples of scales from groups of stocks are obtained annually to develop rules for classifying scales of catch samples to stock groups.

Assessments of stock composition in NBA fisheries would be improved by better coverage of stocks potentially contributing to fisheries and by increasing the number of characters useful for distinguishing among stocks. This feasibility study increased stock coverage over that in which scale-pattern analysis was used but was limited to characters known in earlier years to have shown promise for distinguishing stocks when the catch samples were obtained. Baseline samples of four characters from 73 stocks (55 Canadian and 18 Alaskan) covered all major and many lesser stocks potentially contributing to the fisheries. The four characters of sockeye salmon—two genetically inherited proteins, freshwater age, and a parasite—were examined for their utility in realistic assessments of weekly stock composition in two Alaskan fisheries: Noyes Island in 1986 and Sumner Strait in 1987. All characters were variable among years in their relative frequencies of types within populations; but among the four characters examined, the genetic proteins were probably the most stable among years, and freshwater age, the least stable. Repeated sampling over years indicated that stability of parasite prevalence was more like that of genetic characters than of freshwater age. Reasonably time-stable characters are essential if better baseline coverage of stocks is to be economically feasible.

A dendrogram based on the composite four characters was used to delineate the baseline stocks into 13 groups similar in their characters. All 13 similarity groups are represented in the two major dendrogram branches: the low parasite-prevalence branch and the high parasite-prevalence branch. Prior knowledge of magnitudes of Alaskan and Canadian sockeye salmon stocks, their migration routes, and their estimated contributions to NBA fisheries based on tagging studies of 1982 and 1983 demonstrated that low parasite-prevalence stocks occurring at Noyes Island and Sumner Strait were mainly of Canadian origin. However, high parasite-prevalence stocks could have been of Canadian or Alaskan origin.

Estimated stock compositions at Noyes Island in 1986 and Sumner Strait in 1987 were disparate, as expected from previous scale analyses and tagging studies. Differences in stock composition were most evident from the parasite. The percentage of fish parasitized in weekly samples at Noyes Island ranged from 13 to 34%, and at Sumner Strait, from 65 to 78%. Maximum-likelihood estimates of weekly percentage of Noyes Island catches from low parasite-prevalence stock groups ranged from 78 to 92%, and at Sumner Strait, from 24 to 50%. Estimates of percentages from low parasite-prevalence stock groups represented reasonable minimal estimates of Canadian contributions if low parasite-prevalence north-

ern Southeast Alaskan stocks were rare in NBA fisheries in 1986 and 1987, as in the tagging years of 1982 and 1983.

Numerical studies were conducted in which the percentages of the 13 similarity groups in catch samples from Noyes Island and Sumner Strait were altered by adding random samples of individuals drawn from the baseline stocks. A regression analysis of the estimated changes on the induced changes for the eight weekly samples of either Noyes Island or Sumner Strait showed that the maximum-likelihood method was able to recognize the alteration of the samples. With perfectly time-stable characters, the composition changes were fairly accurately, if imprecisely described.

Numerical studies detected lack of fit of the mixture model to samples of the baseline stocks and catches at both Noyes Island and Sumner Strait. Probably changes in relative frequencies of characters between sampling catches and stocks were largely responsible. Freshwater age appeared responsible for much of the lack of fit of the mixture model to catch and baseline samples, although other characters also likely contributed to the lack of fit.

Two reassessments of stock composition at Noyes Island and Sumner Strait were performed to accommodate the changes in baseline characters. First, both stock composition and parameters describing baseline stock characteristics were estimated by the unconditional maximum-likelihood method. Differences between conditional and unconditional maximum-likelihood stock composition estimates for any of the 13 similarity groups were less than 2% in any week at Noyes Island and less than 4% in any week at Sumner Strait. Second, conditional maximum-likelihood estimates, based on only three characters (freshwater age was omitted), showed minor differences in estimated percentages of combined high or low parasite-prevalence stock groups and, hence, in the proposed minimum estimates of Canadian stock contributions.

Estimates of Alaskan contributions to the catches based on scales were shown to be too high throughout most of the season at both Noyes Island and Sumner Strait unless the parasite prevalence observed in catch samples at both fisheries was not representative of that of the commercial catches or migrations were radically different from those of tagging years. Greater confusion between Alaskan and coastal Canadian salmon scales was expected than between Alaskan and noncoastal Canadian scales, but direct evidence of such error was not found. Rather, many salmon from low parasite-prevalence stocks of Canada (the largest of which were noncoastal) were apparently misclassified as Alaskan stocks when scales were used.

Conclusion

Stock composition of sockeye salmon in two NBA fisheries was assessed with good precision from the four characters studied, if stock detail no finer than that defined by low and high parasite-prevalence branches was required. However, sampling error was generally much larger for some subgroups within these branches. Moreover, contributions of some stock groups were misidentified, and this confusion was likely among similar stock groups within the branches. Since this study began, the baseline has grown both in number of stocks and characters. Many more polymorphic loci that show promise in resolving mixed-stock composition of sockeye salmon in NBA fisheries are now available for the baseline stocks: *PEPC** and *LDH-B1** (Utter et al.[4]); *sIDHP-1**, SIDHP-2*, and *sAAT-1,2** (Wishard[3]); *ALAT** and *sMDH-B1,2** (Grant et al., 1980); *SAAT-3** (Wood et al., 1987a); *LDH-B2** (Hodgins et al., 1969); and *mAAT-1** and ESTD* (Guthrie et al.[7]). Feasibility of a higher resolution of stock contributions by addition of these genetic characters to the baseline will be examined in future studies.

Acknowledgments

The authors thank Chris Wood of the Pacific Biological Station of CDFO for compiling freshwater age samples from fisheries organizations of the United States and Canada and for providing a computer file of the four baseline characters in the analysis. The helpful comments of Norma Jean Sands and Ben Van Alen of ADF&G, Chris Wood, and an anonymous reviewer on an earlier draft are much appreciated.

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